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THE TAXONOMIC STATUS OF THE
SOUTHERN SEA OTTER

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ABSTRACT: A recent review of the taxonomy of the sea otter (*Enhydra lutris*) by Roest (1973) concluded that all populations of this species extending from the Commander Islands to southern California should be considered to constitute a single subspecies (*E. l. lutris*). At present a 1700 mile gap (between Alaska and California) exists within this vast range. We re-examined Roest's data (and the available literature) for evidence which might suggest alternative taxonomic conclusions. In our opinion, the known facts strongly support the conclusion that the southern sea otter should continue to be recognized as a separate subspecies (*E. l. nereis*). Marked morphological and behavioral differences seem to exist, and at the present time complete genetic isolation as well. If a northwest-southeast cline in morphology existed formerly, the evidence suggests that there was a pronounced step or change in its slope in southwestern Alaska.

INTRODUCTION

Merriam (1904) described the Californian population of the sea otter (*Enhydra lutris*) as *Latax lutris nereis* on the basis of morphological differences between a single skull from San Miguel Island, Santa Barbara County, and skulls of typical *E. l. lutris* from the Aleutian Islands, Alaska. The validity of *E. l. nereis* has been variously accepted or questioned by subsequent workers (e. g., Grinnell, 1933; Grinnell, Dixon, and Linsdale, 1937; Scheffer and Wilke, 1950; Hall and Kelson, 1959; Kenyon, 1969). Until recently, lack of adequate material has been a severe handicap to critical evaluation of the taxonomic status of the Californian population. However, Roest (1971) compared large samples of adult skulls of known sex from Alaska (mainly from the Aleutians) and California. On the basis of skull differences and differences between the two populations in

weight and total length, he recognized *E. l. nereis* as valid and as the proper subspecific designation for the southern sea otter. Subsequently additional skulls, from southwestern Alaska, became available to him. These specimens were intermediate in characters between those from the Aleutians and California and he proposed (Roest, 1973) that these characters varied clinally. On that basis he synonymized *E. l. nereis* and included all of the sea otters from the Commander Islands to California in *E. l. lutris*.

On the basis of Roest (1973), Miller (1974, p. 2), in an official publication of the California Department of Fish and Game, stated: "Now that *E. l. nereis* is no longer valid, *the question of sea otters in California being rare or endangered is void inasmuch as there are over 120,000 sea otters now extant in Alaskan waters, and over 1,600 in California*" (italics ours). In other words, according to Miller, the demographic status of the sea otter in California had been decided by the taxonomy proposed by Roest (1973).

Because of the possible importance of the taxonomy of the California sea otter to this animal's rare and endangered status, and to future management decisions, and because of the inherently challenging taxonomic questions involved, we re-examined Roest's data for evidence which might suggest alternative taxonomic conclusions to those chosen by him (1973). We found that there are, in fact, several alternative interpretations of the available data on geographic variation in the sea otter. Moreover, Roest's interpretation does not seem to fit the known facts as well as do other explanations. In the following discussion of geographic variation in *Enhydra lutris*, the subspecies *E. l. gracilis* of the Kurile Islands and the southern tip of Kamchatka is not reviewed critically.

DISCUSSION

Roest (1971) assembled 214 adult sea otter skulls from Alaska, mainly from the Aleutian Islands, and 50 adult skulls from California. He took 24 skull measurements and, on the basis of stepwise discriminant analysis, selected four characters as being of taxonomic significance. Using a combination of these characters applied to skulls of known sex only, he designated each of 156 Alaskan and 40 Californian skulls as "Alaskan" or "Californian," with the following results:

Origin	N	Correctly identified	Incorrectly identified	Not referable
Alaska	156	141 (90.5%)	2 (1.3%)	13 (8.3%)
California	40	38 (95.0%)	0	2 (5.0%)

On the basis of the high degree of separability of Alaskan from Californian skulls, supplemented by differences in total length and in weight between the two populations, Roest recognized *E. l. nereis* as a valid subspecies and applied this name to the southern sea otter.

In 1972, skulls from southwestern Alaska (the Alaska Peninsula, southern Alaska, and Prince William Sound) became available and proved to be intermediate between those from the Aleutians and California (Roest, 1973). On the basis of this sequential shift in skull morphology from west to southeast, Roest proposed that variation in skull characters was clinal and that all of the sea otters from the Commander Islands to California pertain to a single race, *E. l. lutris*. From this viewpoint *E. l. nereis* was relegated to the synonymy of *E. l. lutris* although Roest (1973, pp. 8, 14) noted that the Californian population can be distinguished from the Aleutian population, but not from the population of southwestern Alaska.

There are, however, alternative interpretations of the variation in skull characters from the Aleutians to California. One of these has been suggested to us by Dr. Carl L. Hubbs (pers. comm.). Noting that Roest did not examine skulls from the area between southwestern Alaska and California, he points out that we do not therefore know the nature of variation over this distance of 1700 nautical miles (all distances given are great circle distances unless otherwise specified). Hubbs suggests that variation in skull characters may not have been gradually changing in the way suggested by Roest (1973), but they "may have been fairly constant throughout most of this vast distance; if so, we would have two well marked subspecies with a band of intergradation in southwestern Alaska."

Actually, Roest's own data suggest this. Of ten specimens from near Umnak Island and along the north shore of the Alaska Peninsula, "3 specimens show primarily Alaskan features, 6 are intermediate, and 1 could be considered Californian . . .," whereas of 16 specimens from Prince William Sound, he considered two Alaskan, two intermediate, and 12 Californian (Roest, 1973, pp. 8-9). These distributions differ significantly ($\chi^2 = 10.69$; $P < .01$). This pronounced shift toward the characters of the southern population, so far north in the sea otter's range, suggests that a population with Californian skull characters may well have extended far north into British Columbian waters. This would be quite compatible with Hubbs' suggestion of two well-marked subspecies intergrading in southwestern Alaska rather than clinal variation occurring within a single, widely distributed population.

If variation in skull characters was indeed clinal, there must have been a pronounced step or shift in slope steepness between the Alaska Peninsula and Prince William Sound. The great majority of specimens from Amchitka and Adak are of the Alaskan skull type. Between Adak and Port Heiden, the north-easternmost locality on the Alaskan Peninsula from which Roest had specimens, skull type has shifted from Alaskan to predominantly intermediate over a distance of 695 nautical miles. Between Port Heiden and Prince William Sound skull type has shifted from intermediate to predominantly Californian over a distance of 435 nautical miles. If the samples previously discussed indicate

accurately the morphologic variation in the populations from which they were drawn, the slope of the cline over the 1700 nautical miles from Prince William Sound south to Monterey Bay must have been extremely gentle compared to that from Prince William Sound to Adak.

As regards weight differences between the northern and southern populations, the data presented by Roest (1973, p. 2) suggest that Californian males weigh considerably less than both Aleutian and southwestern Alaskan males; the same is true of females but the difference is less. However, some critical samples are small; further, most of his Alaskan specimens were weighed when fresh and most Californian specimens were weighed some time after death. Additional data on body weights are available from the literature (see summary in Harris, 1968; Kenyon, 1969; Wild and Ames, 1974). However, these do not permit critical geographic comparisons because it is not possible to compare comparable age groups. Nevertheless, they suggest in general that northern otters average heavier and reach a larger maximum weight (100 pounds for males, Kenyon, 1969, p. 21), thus supporting the trend suggested by Roest.

Data on total length (Roest, 1973, p. 7) indicate that males from California are considerably smaller than males from both southwestern Alaska and the Aleutians whereas females from both California and southwestern Alaska are smaller than those from the Aleutians. Unfortunately, total lengths of Alaskan specimens are curvilinear and those of Californian specimens are standard lengths (a fact not mentioned by Roest [1971] although means, ranges, and sample sizes indicate that the same samples were used in both papers). Thus, the generally larger size of Alaskan specimens may be accentuated by the difference in measurement techniques.

Student's *t* tests applied to Roest's 1973 data indicate significant differences in mean total length ($P < .001$) between males from California and males from both Adak and southwestern Alaska. However, males from the last two localities do not differ significantly. The mean length of females from Adak differs significantly from that of females from southwestern Alaska ($P < .01$) and California ($P < .001$), but females from California and southwestern Alaska do not differ significantly.

As regards color, "Alaskan otters are . . . dark, but those from California are most commonly medium brown in color" (Roest, 1973). It is not possible to estimate the degree of separability of the Alaskan and Californian populations on the basis of pelage color from this information, but apparently most southern sea otters can be distinguished by their color. Data summarized by Harris (1968, pp. 263–264) also support this conclusion.

To summarize the morphological data, the sea otter populations of the Aleutians and California can be differentiated at a level of better than 90% on the basis of skull characters. Aleutian otters are also larger and darker than those from California. Between these populations there is a population in southwestern

Alaska with intermediate skull characters; the males are larger than those from California but the females are similar in size. It is impossible, on the basis of available material, to determine with confidence whether the population in southwestern Alaska represents a point on a long west-southeast cline or whether it is a population intergradient between well-marked northern and southern subspecies. If, however, this population is on a cline, there must be a pronounced step or change in slope steepness between the Alaska Peninsula and Prince William Sound.

In addition to morphological differences, there are also behavioral differences between northern and southern sea otters. The use of hard objects placed on the chest as anvils for breaking open hard-shelled food items is rare in the otters of the Commander Islands and Amchitka, but is common in the otters of California. Since the diet of Alaskan otters includes a much higher proportion of fish than does the diet of southern otters, there may be simply less need for tool-using in the northern part of the species' range.

Hauling out on land is much more frequent in the northern population. In apparent association with this increased use of land is more efficient terrestrial locomotion in Alaskan otters. Kenyon (1969) states that northern otters walking unhurriedly move with a rolling gait, raising one foot at a time. When animals are startled "they arch the back and bound or hop, moving both forefeet then both hind feet forward in rapid succession. Speed of movement is somewhat less than the running speed of a normally agile man." In contrast, Californian otters do not arch the back and do not move their appendages alternately. Rather, "they either drag their hind quarters or repeatedly pivot their bodies up and forward with the help of their feet" (J. Vandevere, paper presented at AAAS meeting, San Francisco, California, 27 February 1974). These differences suggest possible genetic differences in both behavior and anatomy between northern and southern sea otters. In this regard it is of considerable interest that the Asian sea otter (*E. l. gracilis*) is also relatively clumsy on land (Lydekker, 1895; Barabash-Nikiforov, 1947).

The ability of Alaskan sea otters to move relatively long distances out of water has been documented by Schneider and Faro (1975). In 1971 a number of otters were trapped by rapidly forming pack ice along the north shore of the Alaska Peninsula, and a number died because they could find no open leads in which to forage. Two dead sea otters were found 8 km. inland from Port Heiden Bay and one dead otter was seen "15 km inland, half way to Pavlof Bay on the Pacific Ocean." These animals may have been trying to reach the Pacific Ocean in an attempt to find open water where foraging was possible.

Vandevere (1970) described a number of differences in reproductive behavior between northern and southern sea otters. Most striking of these were differences in the posture of the female during copulation. The sequence of events leading to copulation also differed, the nose or side of the face of the female being grasped

by the northern male rather late in precopulatory struggling whereas this occurs early in this stage of copulation in southern otters.

The present distribution of the southern sea otter in relation to its nearest conspecifics is also of critical importance in assessing the distinctiveness of this population. As of early December 1974, the northernmost established Californian sea otters were located off Sunset State Beach, Santa Cruz County, about 15 airline miles south-southeast of the city of Santa Cruz. A few individuals have been seen north of this point but none has stayed long enough to suggest establishment. The nearest naturally occurring northern sea otters are in Prince William Sound, 1700 nautical miles to the north, although Pedersen and Stout (1963) reported the sighting of what was probably a single otter off Neahkahnie, northern Oregon, between August 1961 and February 1962. A small introduced population is located near Port Orford, Oregon, 365 nautical miles to the north, where a number of otters from Amchitka were released in 1970 and 1971; about 23 are still present.

At this time, the southern sea otter is well removed from its nearest conspecifics and there is no exchange of genetic material between this population and any other. Since 1914, the sea otter has extended its range north in California from Point Sur, Monterey County (Wild and Ames, 1974, p. 23, fig. 5) to Sunset State Beach, a great circle distance of only 35 nautical miles in 60 years. The isolation of the Californian population is thus likely to continue for many years if the present natural situation persists.

Although complete disruption of gene flow between Californian and other sea otters may be relatively recent, resulting from the decimation of the species by fur traders in the last two centuries, the severe reduction of the southern population may well have had profound effects on its genetic constitution. This is strongly suggested by the findings of Bonnell and Selander (1974) on the northern elephant seal (*Mirounga angustirostris*). Electrophoretic analysis of blood samples from five isolated breeding colonies in California and Mexico indicated no polymorphisms among 21 proteins encoded by 24 loci. The authors concluded that this homozygosity may have resulted from fixation of alleles brought about by the decimation of the species by sealers in the 19th century. Although comparable evidence is not available for the sea otter, it seems highly likely that the severe reduction in numbers suffered by the southern population, followed by strong geographic isolation, has had some effect on that population's genetic constitution.

CONCLUSIONS

In the application of formal scientific nomenclature to naturally occurring populations, the taxonomist frequently faces the problems inherent in trying to fit a myriad of biological situations into the rigid framework of a fixed nomen-

clatural system. The best that one can do is to use that nomenclature which best expresses the natural situation with which he is dealing.

In the case of the sea otter, at least two interpretations may be made of the morphological variation observed in the populations between the Commander Islands and Monterey Bay. If we regard this variation as clinal, then the nature of the cline must influence our choice of nomenclature. Three characteristics of this presumed cline are of particular importance: 1) the terminal populations are separable at a level of at least 90% on the basis of skull morphology; 2) there is either a step in the cline, or a pronounced change in slope steepness, between the Alaska Peninsula and Prince William Sound; 3) the population at the southern terminus has been much reduced and has been completely isolated for at least 100 years, with a strong possibility that its genetic constitution has undergone significant change.

Given these characteristics, whether one includes the entire cline in a single subspecies or treats the terminal populations as distinct subspecies becomes a matter of professional judgement. If we are dealing with a case of primary intergradation in which a gradual cline along western North America sharply changes slope in southern Alaska, it may still be appropriate scientifically to recognize the northern and southern sea otters as distinct subspecies. There are many instances in vertebrate taxonomy in which the terminal populations of a cline are regarded as distinct subspecies if they are distinctly separable in a variety of traits, and/or if they are separated by a pronounced step in the cline. If, in fact, variation is actually clinal in this way, it is just as proper taxonomically to regard the northern and southern sea otters as distinct subspecies as it is to combine them in *E. l. lutris*.

However, it is by no means clear that we are dealing with a case of primary intergradation. It is equally possible that there are two distinct subspecies which in recent history intergraded (secondarily) in southwestern Alaska and, indeed, this is strongly suggested by the nature of the variation described by Roest in the samples available to him. Moreover, some taxonomists have advocated that subspecies designations be applied only to portions of species which are not only genetically distinct, but which are at least partially independent (separately evolving) evolutionary units (e.g., Lidicker, 1962). The southern sea otter clearly meets even these stringent criteria by virtue of its genetic isolation, its morphological and behavioral differentiation, and its recent derivation from what must have been an extremely small remnant population. Further, there are important differences between the habitats occupied by the northern and southern sea otters. Formation of pack ice as described by Schneider and Faro (1975) never occurs within the range of the southern population. Water temperatures are much lower in the north. Daily sea-water surface temperatures at Scotch Cap in the Aleutians over a five-year period ranged from -1.39°C to 12.22°C , and at Monterey, California, over a similar period, they ranged from 10.1°C to 16.7°C

(Ricketts and Calvin, 1948, p. 263, fig. 117). Many other habitat differences undoubtedly occur as well. All of these factors imply that the two otter populations are subjected to quite different selective regimes.

Thus, whether one views the evidence as indicating that the southern sea otter population is part of a stepped cline, a remnant of two historically well marked subspecies intergrading in southwestern Alaska, or a recently differentiated and unique evolutionary unit, its formal designation as a subspecies is justified on scientific grounds. Given that such designation is scientifically sound, one may still ask what are the advantages and disadvantages to advocating this nomenclatural arrangement.

There seems to be no particular advantage to including these populations in one subspecies, but there are a number of disadvantages to doing so. This course of action would conceal the high degree of separability between the southern and northern populations; it would conceal the pronounced step or shift in slope in the indicated cline in southern Alaska; it would fail to consider certain behavioral differences, and possible related anatomical differences, between the northern and southern populations; and it would give no idea of the present geographic isolation of the southern population. To us, formal recognition of the southern population as a distinct subspecies, to which the already available name *E. l. nereis* may be applied, much more accurately reflects the existing natural situation than would any other nomenclatural arrangement. Furthermore, it is an arrangement which is consistent with recognition of the Asian subspecies *E. l. gracilis* (cf. Barabash-Nikiforov, 1947; Roest, 1973), a form which appears to be of comparable distinctiveness to *E. l. nereis* (differing in size, cranial features, pelage color, and behavior), but much less isolated by distance. We therefore propose that three subspecies continue to be recognized for this unique and important mammal.

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